Oikos 125: 726–734, 2016
doi: 10.1111/oik.02742

Subject Editor: Matty Berg. Editor-in-Chief: Dries Bonte. Accepted 17 August 2015

Termite mounds differ in their importance for herbivores across savanna types, seasons and spatial scales

Andrew B. Davies, Shaun R. Levick, Mark P. Robertson, Berndt J. van Rensburg, Gregory P. Asner and Catherine L. Parr

A. B. Davies (adavies@carnegiescience.edu) M. P. Robertson, Centre for Invasion Biology, Dept of Zoology and Entomology, Univ. of Pretoria, Pretoria, 0002, South Africa. Present address for ABD: Dept of Global Ecology, Carnegie Inst. for Science, 260 Panama Street, Stanford, CA, USA. – S. R. Levick, Max Planck Inst. for Biogeochemistry, Hans-Knöll Street 10, Jena, DE-07745, Germany. – B. J. van Rensburg, School of Biological Sciences, Univ. of Queensland, St. Lucia, QLD 4072, Australia, and: Centre for Invasion Biology, Dept of Zoology, Univ. of Johannesburg, Auckland Park, Johannesburg, 2006, South Africa. – G. P. Asner, Dept of Global Ecology, Carnegie Inst. for Science, 260 Panama Street, Stanford, CA 94305, USA. – C. L. Parr, School of Environmental Sciences, Univ. of Liverpool, Liverpool, L69 3GP, UK.

Herbivores do not forage uniformly across landscapes, but select for patches of higher nutrition and lower predation risk. *Macrotermes* mounds contain higher concentrations of soil nutrients and support grasses of higher nutritional value than the surrounding savanna matrix, attracting mammalian grazers that preferentially forage on termite mound vegetation. However, little is known about the spatial extent of such termite influence on grazing patterns and how it might differ in time and space. We measured grazing intensity in three African savanna types differing in rainfall and foliar nutrients and predicted that the functional importance of mounds for grazing herbivores would increase as the difference in foliar nutrient levels between mound and savanna matrix grasses increases and the mounds become more attractive. We expected this to occur in nutrient-poor areas and during the dry season when savanna matrix grass nutrient levels are lower. Tuft use and grass N and P content were measured along transects away from termite mounds, enabling calculation of the spatial extent of termite influence on mammalian grazing. Using termite mound densities estimated from airborne light detection and ranging (LiDAR), we further upscaled field-based results to determine the percentage of the landscape influenced by termite activity. Grasses in close proximity to termite mounds were preferentially grazed at all sites and in both seasons, but the strength of mound influence varied between savanna types and seasons. In the wet season, mounds had a relatively larger effect on grazers at the landscape scale in the nutrient-poor, wetter savanna, whereas in the dry season the pattern was reversed with more of the landscape influenced at the nutrient-rich, driest site. Our results reveal that termite mounds enhance the value of savanna landscapes for herbivores, but that their functional importance varies across savanna types and seasons.

Herbivores do not forage uniformly across landscapes, but respond to spatial and temporal heterogeneity, selecting patches with enhanced nutrition and lower predation risk (Owen-Smith 2002, Anderson et al. 2010, Hopcraft et al. 2010). Some nutrient-rich sites, such as grazing lawns (short grass areas with heavy grazing pressure) are maintained by the herbivores themselves (Archibald 2008), whereas abiotic processes are more important in the establishment and persistence of others, e.g. sodic sites (low-lying areas with high sodium levels) (Grant and Scholes 2006). At fine spatial scales, biotic structures such as large trees (Treydte et al. 2011) and dung middens (Cromsigt and Olff 2008) create nutrient-enriched sites that are attractive to herbivores. Through termite activity (the redistribution and concentration of soil nutrients, organic material and moisture), epigeal termite mounds are rich in nutrients and have higher levels of soil moisture, supporting compositionally distinct, nutrient-enriched plant communities on and around them (Traoré et al. 2008, Moe et al. 2009, Erpenbach et al. 2013, Davies et al. 2014b). These vegetation communities result in termite mounds becoming foraging hotspots, favoured by a diverse range of browsing and grazing herbivores (Loveridge and Moe 2004, Mobæk et al. 2005, Levick et al. 2010b).

However, two recent studies have challenged this generally accepted rule of enhanced browsing on termite mound vegetation. Muvengwi et al. (2013) documented higher elephant browsing on savanna matrix vegetation than on termite mounds, and, elsewhere, tree species preferred by browsers were found to be more prevalent in the savanna matrix (Van der Plas et al. 2013). These findings are attributed to the relatively nutrient-rich context of the study sites, resulting in little nutritional difference between mound and matrix vegetation. The role of termite mounds in driving savanna heterogeneity and their importance as foraging hotspots might therefore depend on landscape context, with mounds being less important to herbivores in nutrient-rich savannas.

Differences in vegetation community composition between termite mounds and the savanna matrix become increasingly pronounced with increasing mean annual precipitation (Erpenbach et al. 2013, Davies et al. 2014b). Due to soil leaching and greater denitrification (especially pyrodenitrification), wetter savannas are generally nutrient-poor relative to drier ones (Scholes 1997), leading to more pronounced nutritional and compositional differences between mound and savanna matrix vegetation (Davies et al. 2014b). These findings highlight the need for studies across environmental gradients if we are to understand the role of termite-driven heterogeneity in shaping herbivore feeding patterns.

Differences in the importance of mounds for herbivores are likely to be reflected in the size of the sphere of influence around termite mounds (i.e. the area around the mound influenced by the mound). Where mounds are less important to herbivores (e.g. high-nutrient savannas), lower grazing pressure and a smaller area of intense herbivory around them is expected as the grasses in the adjacent savanna matrix will provide sufficient nutrition. The majority of studies have, however, only compared herbivory on and off mounds, with limited information available on the extent of mound influences. Similarly, there is a poor understanding of the landscape-level effects induced by mounds, with most studies focused on small-scale, local effects around individual mounds, making it difficult to extrapolate findings up to regional or landscape levels. Browsing intensity has been shown to be negatively correlated with distance from mound centres (Loveridge and Moe 2004) and these browsing effects may be extensive, influencing as much as 20% of the landscape (Levick et al. 2010b). Although the spatial extent of mound influence on savanna grass diversity has been quantified (Davies et al. 2014b), the spatial extent of grazing patterns and how these translate to landscape scale effects have yet to be investigated.

On a temporal basis, mounds have been suggested to sustain mammalian herbivore populations through the dry season because their vegetation contains essential nutrients throughout the year, as opposed to the savanna matrix vegetation that is only nutritious enough during the wetter months (Grant and Scholes 2006). Mounds are therefore predicted to be used more heavily during the dry season, but whether this pattern is consistent across nutritionally different savanna types has not been adequately tested. Although use of termite mound vegetation is expected to increase in the dry season, such increases are likely to be less pronounced in nutrient-rich savannas where the savanna matrix contains more available nutrients for herbivore populations. In contrast, wetter, nutrient-poor savannas may have less available nutrition during the dry season when savanna vegetation deteriorates in both quantity and quality, with mounds becoming essential nutrient hotspots for herbivore populations.

Here, we investigate the effects of *Macrotermes* mounds on grazing patterns at three savanna sites differing in rainfall and nutrient quality. We combine herbivory data with grass foliar nutrient data to examine possible mechanisms for the observed patterns. Specifically, we aimed to determine how the spatial extent of grazing on termite mound vegetation varies with savanna type and season (wet versus dry) at both the local and landscape scale (i.e. we documented grazing around individual mounds and scaled these findings up to the regional landscape, providing the first assessment of the percentage of landscapes influenced by mound-induced grazing). Across all sites, we expected greater grazing on mound vegetation than in the surrounding savanna matrix due to higher quality forage on mounds, and we expected this to be particularly pronounced in the dry season when forage is scarce. We also anticipated that mounds would be relatively more important for grazers in wetter, nutrient-poor savannas because there is a greater difference in forage quality on and off mounds here.

Methods

Study site

The study took place in three savanna vegetation types in southern Kruger National Park (KNP), South Africa. The three sites occur in a summer rainfall region and vary in mean annual precipitation, vegetation characteristics and herbivore biomass. The driest site (Skukuza, 25°02′ S, 31°30′ E) is considered a relatively nutrient-rich savanna (sweet veld) characterised by an *Acacia nigrescens/Combretum apiculatum* association (Gertenbach 1983) and receives a mean rainfall of 550 mm year^{-1} (Zambatis 2003). The dominant grasses on termite mounds are *Panicum maximum* and *Urochloa mosambicensis*, whereas in the matrix *P. maximum*, *Pogonarthria squarrosa*, *Digitaria eriantha* and *Brachiaria nigropedata* are common (Davies et al. 2014b). The wettest site (Pretoriuskop, 25°12′ S, 31°16′ E) is dominated by *Terminalia sericea* and *Dichrostachys cinerea* and is considered to be relatively nutrient-poor (sour veld) (Gertenbach 1983); grasses on mounds are dominated by *Cynodon dactylon* and *P. maximum*, whereas the matrix is characterised by *Setaria sphacelata*, *Loudetia simplex*, *P. squarrosa* and *Schizachyrium sanguineum* (Davies et al. 2014b). Mean annual rainfall here is 750 mm year^{-1} (Zambatis 2003). An intermediate site (Napi, 25°06′ S, 31°27′ E) is located between these two distinct regions and contains a mosaic of the two vegetation types, with *Combretum zeyheri* and *C. collinum* being dominant tree species (Gertenbach 1983). Rainfall here is also intermediate, ca 625 mm year^{-1} (Zambatis 2003). Common grasses on mounds are *P. maximum* and *U. mosambicensis*, whereas in the matrix *D. eriantha*, *Eragrostis rigidior* and *P. squarrosa* dominate (Davies et al. 2014b). All three sites occur within an undulating landscape on granitic substrate; *Macrotermes* mounds occur predominantly on crests and upper sections of hillslopes (Levick et al. 2010a, Davies et al. 2014a).

Primary grazers and mixed-feeders in the study area include white rhinoceros *Ceratotherium simum*, Cape buffalo *Syncerus caffer*, plains zebra *Equus quagga burchellii*, blue wildebeest *Connochaetes taurinus*, impala *Aepyceros melampus*, elephant *Loxondonta africana* and waterbuck *Kobus elipsiprimnus*. Herbivore biomass at each site was calculated from KNP aerial census data collected between 1987 and 1993 when high spatial resolution sampling was conducted (Smit et al. 2007). Biomass values for grazers and mixed-feeders were obtained from the six one decimal degree

grid cells (each 1 km^2 in extent) closest to the termite mound locations (covering the area and immediate surrounds of the ten termite mounds surveyed in each savanna site) and a mean value for each savanna site calculated (Table 1). After 1993, the aerial census technique changed in KNP to a sample-based, distance sampling approach with the resultant resolution too coarse for use in this study. However, apart from the cessation of elephant culling in 1994 (Whyte et al. 2003), management of large herbivores has not changed since 1993, and apart from elephant and white rhino numbers increasing, populations of other herbivores have remained relatively stable across the park (SANParks unpubl.). Herbivore density patterns, and particularly the relative densities between our three study sites, were therefore expected to be similar to those of 1993.

Grazing intensity surveys

Forty termite mounds, spaced at least 50 m apart (and in most cases over 100 m apart), were selected at each savanna site. All surveyed mounds were located on crests (where mounds are almost exclusively found, Levick et al. 2010a, Davies et al. 2014a) and built by *Macrotermes*, with the dominant species in the area being *M. falciger* and *M. natalensis* (Davies et al. 2014a). Mound diameter was measured for each mound along the north–south and east–west axes and the average diameter calculated from these measurements. Grass communities on the selected termite mounds were surveyed by Davies et al. (2014b).

Grazing on and around termite mounds was quantified using two methods. First, grass tuft use was estimated at ten of the forty termite mounds at each site during early April 2012 (the end of wet (growing) season when forage is abundant) and early September 2012 (the end of the dry season when food for grazers is most limited). However, due to a natural fire that burnt all vegetation at the intermediate site in August 2012, September surveying was conducted for the driest and wettest sites in 2012 and for the intermediate site a year later in September 2013. Fires are a common occurrence in southern African savannas and highly variable in KNP, resulting in a patch mosaic of fire histories and the majority of the landscape having burnt relatively recently (the mean fire return interval is 4.5 years, van Wilgen et al. 2000). Although fire is known to affect herbivore foraging and distributions (Archibald and Bond 2004), effects of single fire events on vegetation cover do not last longer than a few months, following which vegetation regrows and differences rapidly disappear (Parr et al. 2004, Radford and Andersen 2012). Therefore, we do not consider the fire to have adversely affected our results for the dry season (September) sampling since the data were collected 13 months after the fire, with an entire growing season in between the fire and sampling period. Tuft use was estimated by laying out distance transects in the four cardinal directions around each surveyed termite mound. On each distance transect, 4 m line transects (parallel to each other and perpendicular to the distance line transect) were placed at seven distance categories starting on the mound, and then at a distance of 1 m, 2 m, 4 m, 8 m, 16 m and 32 m from the mound (Supplementary material Appendix 1 Fig. A1). Grazing pressure was expected to be higher closer to mounds; hence a geometric progression with the common ratio of 2 was selected for the distance transects. Along each 4 m line transect, the tuft of grass located closest to each 40 cm mark was identified and scored according to grazing intensity, thus 11 tufts per 4 m line transect were assessed, 308 tufts per mound. Scoring was according to the following scale: 0 = no grazing evident, 1 = very light grazing, 2 = light to moderate grazing, 3 = moderate to heavy grazing, 4 = heavy grazing and 5 = tuft completely grazed, only roots remaining. In order to avoid any observer bias, the same observer ranked each tuft of grass throughout the study.

Second, the extent of heavy grazing leading to grazing lawn establishment was measured around termite mounds. For this aspect of the study, 30 mounds in each savanna site were surveyed. Grazing lawns (Hempson et al. 2014) were

Table 1. Characteristics of the three savanna sites surveyed.

	Savanna site		
	Skukuza	Napi	Pretoriuskop
Mean annual rainfall (mm year^{-1})	550	625	750
Foliar nitrogen (mg kg^{-1}) (termite mounds, savanna matrix)	17175 (1.72%), 12362 (1.24%)	18483 (1.85%), 10077 (1.01%)	15159 (1.52%), 8751 (0.88%)
Foliar phosphorous (mg kg^{-1}) (termite mounds, savanna matrix)	1643 (0.16%), 1217 (0.12%)	1911 (0.19%), 1132 (0.11%)	1486 (0.15%), 770 (0.08%)
Mammalian herbivore biomass (kg km^{-2}) for grazers and mixed feeders	1568	3490	838
Macrotermes mound density (mounds ha^{-1})	1.55	0.63	1.37
Dominant tree species	*Acacia nigrescens* *Combretum apiculatum*	*Combretum zeyheri* *Combretum collinum*	*Terminalia sericea* *Dichrostachys cinerea*
Dominant grass species on termite mounds	*Panicum maximum* *Urochloa mosambicensis*	*Panicum maximum* *Urochloa mosambicensis*	*Cynodon dactylon* *Panicum maximum*
Dominant grass species in the savanna matrix	*Panicum maximum* *Pogonarthria squarrosa* *Digitaria eriantha* *Brachiaria nigropedata*	*Digitaria eriantha* *Eragrostis rigidior* *Pogonarthria squarrosa*	*Setaria sphacelata* *Loudetia simplex* *Pogonarthria squarrosa* *Schizachyrium sanguineum*

defined as the area where the biomass of the grass layer was noticeably reduced due to grazing (distinguished by careful examination of tufts, Supplementary material Appendix 1 Fig. A2). Beginning in May 2012, grazing lawns were measured in the four cardinal directions from termite mounds. Measurements were then taken approximately bimonthly until April 2013. However, due to the natural fire in August 2012, measurements at the intermediate site (Napi) were not recorded for September and December 2012.

Nutrient samples

Grass samples from six termite mounds at each savanna site were collected for measurements of nitrogen and phosphorous content. N and P were chosen because they are important nutrients for wild mammalian herbivores (Owen-Smith and Novellie 1982, Grant and Scholes 2006). Tissue samples were collected from the mound and at each distance category along the distance transect used for tuft use measurements. Grass samples were representative of all species present in a 1 m by 1 m quadrat at each distance category with the amount of each species harvested in proportion to its abundance in the quadrat. All samples consisted of above-ground live grass material (no forbs, woody plants or litter) and were collected in January 2012, the peak of the summer growing season. Grass samples were homogenised and analysed spectroscopically for nutrient content at the Max Planck Institute for Biogeochemistry, Jena, Germany.

Data analysis

All statistical procedures were conducted using R software version 2.15.1 (<www.r-project.org>). For each grazing response variable (tuft use and grazing lawn extent), a candidate set of generalised linear mixed-effects models with Poisson error distributions was constructed to examine relationships between the response variable and the factors tested. For tuft use these factors were savanna site, distance from termite mound and season. For grazing lawns the factors were savanna site and time of year (month). Models were applied using the *lme4* package in R (Bates et al. 2007) and ranked according to sample-size-corrected AIC*c* (Burnham and Anderson 2002) using the R package *MuMIn* (Barton 2010), with the best model for each response variable selected for further data analysis. The most parsimonious models for each response variable, ranked according to AIC*c*, are provided in Supplementary material Appendix 1 Tables A1–A2. Effects of each fixed effect present in the most parsimonious model were examined using type III likelihood-ratio χ^2-tests with the R package *car* (Fox et al. 2009). For the tuft use dataset, the 4 m line transect that each tuft was associated with was considered a random effect and nested within the relevant termite mound. For grazing lawn extent, termite mound identity was considered a random effect. After application of the most parsimonious model, multiple comparisons of means post hoc testing for mixed-effects models, using Tukey contrasts averaged across interaction terms when present, was used to examine pairwise comparisons with the R packages *multcomp* (Hothorn et al. 2008) and *mvtnorm* (Genz et al. 2011).

Similarly, for the grass nutrient data (N and P), candidate sets of linear mixed-effects models (P) and generalised (Poisson error distribution) linear mixed-effects models (N) were constructed, with the termite mound identity used as the random effect. The most parsimonious model for each data set (nutrient) was selected using AIC*c* and used for further analysis, with multiple comparisons of means post hoc testing conducted on the fixed effects using Tukey contrasts averaged across interaction terms when present (P).

To determine the spatial extent of termite mound influence on grazing patterns for each savanna site and in each season (April and September) separately, a generalised linear mixed-effects model with distance as a fixed factor was applied to each tuft use data set in order to determine spatial thresholds in the intensity of tuft use. Transect identity, nested within mound identity were random factors in each model. Following this, multiple comparisons of means post hoc testing for mixed-effects models (using Tukey contrasts) was used to examine pairwise comparisons and detect thresholds for each site and season, which were designated as the distance where significant differences between distance categories no longer occurred. Once determined, this sphere of influence (SoI) was assumed to be circular, and the mean area influenced by termite mounds calculated per site and season. This was achieved by adding the extent of grazing (the site and season specific threshold distance) to the diameter of each of forty individual mounds, thereby calculating the SoI around each mound. The mean SoI per site and season was then calculated from these mounds. Using LiDAR imagery from the Carnegie Airborne Observatory (CAO), mound densities on crests in each study area were estimated (Davies et al. 2014a) , and from this the proportion of area influenced by mounds in terms of grazing patterns was calculated for each study site. Due to the nature of remote sensing techniques, some small mounds (< 0.5 m in height) will escape detection; these estimations should therefore be considered as minimum values.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.b0b1c> (Davies et al. 2015).

Results

Grazing and nutrient patterns around individual mounds

Grazing intensity differed significantly between savanna sites ($\chi^2 = 6.62$, $p < 0.05$) and with increasing distance from termite mounds ($\chi^2 = 664.45$, $p < 0.001$), and there was a significant interaction between distance and site ($\chi^2 = 109.58$, $p < 0.001$). Therefore, tuft use decreases with distance from mounds at all sites, but the manner in which it does so differs with savanna site. Multiple comparisons revealed that tuft use was significantly higher on mounds than at distances of 2 m and greater from mounds, and was highest 1 m away from mounds at the driest and intermediate sites ($p < 0.001$). Tuft use was consistently lower at each

subsequent distance category and significantly so up to 16 m from mounds (i.e. there was significantly lower tuft use at 4 m compared to 2 m ($p < 0.001$), again lower at 8 m compared to 4 m ($p < 0.001$) and lower at 16 m compared to 8 m ($p < 0.001$)). Differences in tuft use between 16 m and 32 m were not significant ($p = 0.613$); suggesting that a levelling off of tuft use occurs 16 m into the matrix (Fig. 1).

The highest levels of tuft use on mounds were recorded at the intermediate site, Napi, where there was also the greatest difference in tuft use between mound and savanna matrix grass (Fig. 1). Use levelled off closer to mounds at the driest site, Skukuza, (between 4 and 8 m during the wet season, Fig.1a) where the highest levels of matrix grazing occurred. The wettest site, Pretoriuskop, had the lowest levels of grazing on mounds and in the matrix (Fig. 1).

Foliar nitrogen and phosphorous declined with distance from termite mounds. The strongest declines occurred between mounds and distances 2 m off mounds. (Fig. 3, Supplementary material Appendix 1 Table A3). Site was present in the most parsimonious models for both N and P, with nutrient concentrations being highest at Skukuza and Napi on termite mounds, and highest at Skukuza in the savanna matrix, followed by Napi and then Pretoriuskop (Fig. 3, Supplementary material Appendix 1 Table A4). An interaction term (although not significant) between site and distance was present in the most parsimonious model for P (which declined slower with distance from mounds at Napi than the other sites), but not for N.

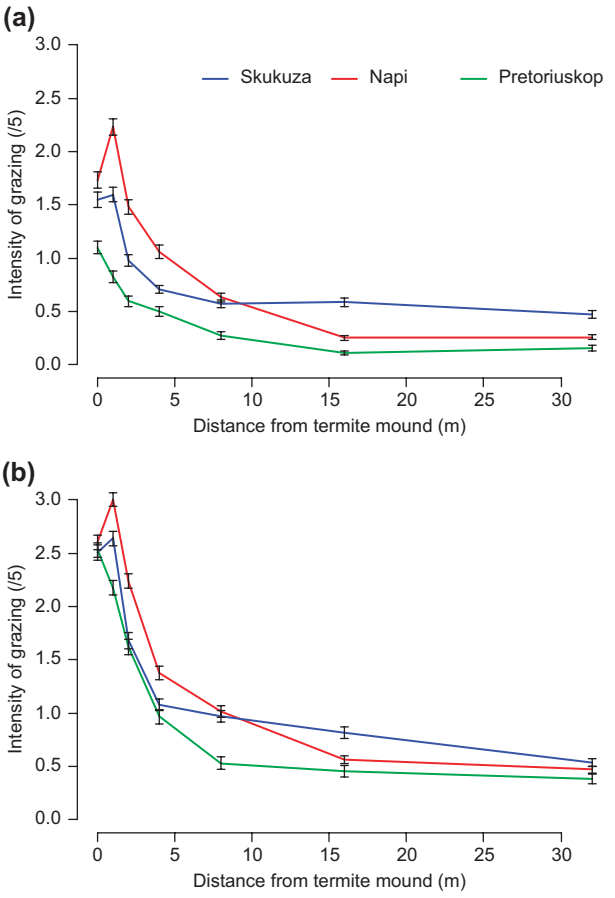

Figure 1. Intensity of grass tuft use along distance transects around termite mounds at three savanna sites during two seasons, (a) the end of the wet season (April) and (b) the end of the dry season (September). Grass tufts were ranked on a scale of 0–5 depending on the intensity of grazing. Sites are arranged (Skukuza to Pretoriuskop) in ascending order of mean annual precipitation received. Error bars indicate standard error.

Seasonal effects on mound grazing

Recorded tuft use was significantly higher during the dry season (September) at all sites ($\chi^2 = 75.35$, $p < 0.001$) and there was a significant interaction between season and site ($\chi^2 = 36.58$, $p < 0.001$), with larger seasonal differences present at Pretoriuskop (particularly for mound grazing) (Fig. 1). During the wet season, tuft use around termite mounds was significantly greater, up to 16 m into the savanna matrix at both Napi and Pretoriuskop and 4 m at Skukuza (Fig. 1a). In the dry season, this increased at Skukuza, up to 16 m, decreased at Pretoriuskop to 8 m and remained the same (16 m) at Napi (Fig. 1b). The extent of heavy grazing leading to grazing lawns around mounds also varied significantly with savanna site and season (sampling month) (site: $\chi^2 = 33.21$, $p < 0.001$; season: $\chi^2 = 9959.35$, $p < 0.001$). Grazing lawns were significantly and consistently larger at Napi than the other two sites ($p < 0.01$ for both comparisons). Differences between Skukuza and Pretoriuskop fluctuated with season, with similar sized lawns in the dry season (May–September) at both sites, but larger lawns at Skukuza during the wet season (December–April). Across sites, lawns displayed significant differences across all sampling months ($p < 0.001$) and were larger during the drier months, with lawn extent peaking in the late dry season (September) (Fig. 2).

Landscape-level effects of termite mounds on grazing patterns

The sphere of influence around mounds, and hence proportion of the landscape affected by termite mounds, was more extensive during the wet season at the wettest site, Pretoriuskop, where approximately 22% of the savanna crest landscape was affected (Table 2). Although individual mounds had the largest sphere of influence at Napi, the overall landscape effect (~11% of the landscape) was smaller than Pretoriuskop due to lower mound densities. Skukuza had the smallest extent of landscape affected (~8%) because although mounds here were larger and occurred at higher

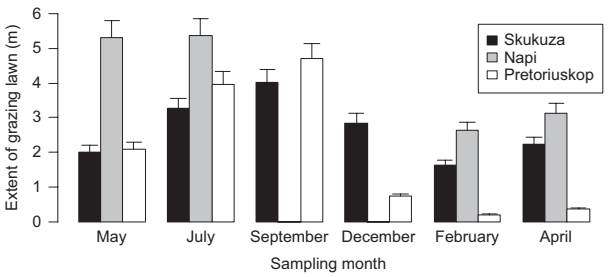

Figure 2. Extent of grazing lawns around termite mounds at three savanna sites across six sampling periods from May 2012 to April 2013. Sites are arranged (Skukuza to Pretoriuskop) in ascending order of mean annual precipitation received. Error bars indicate standard error.

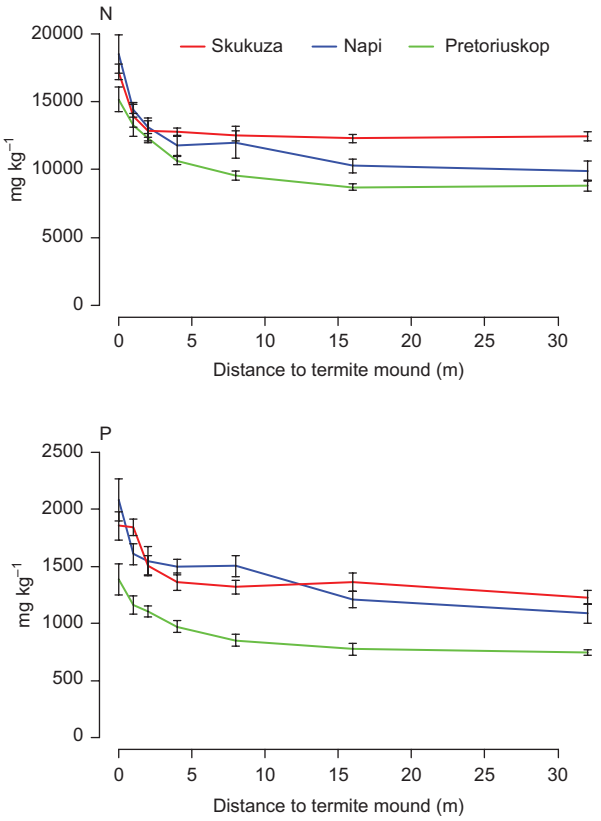

Figure 3. Nitrogen and phosphorus quantity (mg kg^{-1}) from grass tissue samples collected across distance transects away from termite mounds in three savanna sites. Data were pooled from homogenised samples taken from the four cardinal directions around mounds. For significant differences see Supplementary material Appendix 1 Tables A3–A4. Sites are arranged (Skukuza to Pretoriuskop) in ascending order of mean annual precipitation received. Error bars indicate standard error.

densities, the sphere of influence extended to only 4 m from mounds, compared to 16 m at the wetter sites (Table 2). However, during the dry season this pattern was reversed, with mounds at Skukuza influencing almost 30% of the landscape, whereas at Pretoriuskop only about 9% was affected. The area influenced at Napi did not differ between seasons (Table 2).

Discussion

Although our results confirm previous studies that report termite mounds as favoured foraging hotspots for grazing herbivores (Mobæk et al. 2005, Grant and Scholes 2006), demonstrating the importance of these biotic drivers for savanna spatial heterogeneity, our study reveals the extent to which these patterns vary in different savanna types and between seasons. We further demonstrate, for the first time, the large-scale and pervasive influence termites have by affecting grazing patterns at a landscape scale.

Termite mounds have been shown to harbour significantly different grass assemblages (Arshad 1982, Jouquet et al. 2004, Moe et al. 2009, Davies et al. 2014b), which are also higher in nutritional content (Grant and Scholes 2006, Davies et al. 2014b) than the matrix. In our study, grass on

Table 2. The mean area (sphere of influence [SoI]) around individual termite mounds (n = 10 for each savanna site) and the percentage of the landscape within which grazing is enhanced, based on tuft use. The mound densities from which the percentage figures are calculated were attained from LiDAR terrain data and reflect densities on crests within the landscape, the landscape percentage influenced subsequently refers to percentages of crests influenced by mounds.

Savanna site (season)	Mean SoI around individual mounds (m^2)	Mound density (ha^{-1})	Landscape percentage influenced by mounds
Wet season			
Skukuza	478.7	1.6	7.7
Napi	1800.4	0.6	10.8
Pretoriuskop	1540.6	1.4	21.6
Dry season			
Skukuza	1847.8	1.6	29.6
Napi	1800.4	0.6	10.8
Pretoriuskop	630.9	1.4	8.8

termite mounds and 1 m off mounds at all three savanna sites contained higher levels of both N and P, essential nutrients for mammalian herbivores (Owen-Smith and Novellie 1982, Grant and Scholes 2006), than the savanna matrix, suggesting that enhanced foliar nutrition is driving increased levels of herbivory. However, termite mounds also contain higher levels of soil moisture than surrounding savanna soils, benefitting plants and possibly also attracting grazers. Water content is particularly high around the base of termite mounds (Arshad 1982, Dangerfield et al. 1998), possibly explaining the increased grazing 1 m from mound edges at the driest and intermediate sites, despite higher grass nutrient levels on mounds. Termite mounds at these sites are also taller and steeper compared to Pretoriuskop (Davies et al. 2014a), likely increasing water run-off to mound bases. However, their height and steepness might also preclude on-mound grazing and cause herbivores to instead graze around them.

Influence of individual mounds: variation among sites

Site differences in the ratio of termite mound to savanna matrix tuft use suggest that the relative importance of mounds for savanna herbivores is not consistent, but varies with savanna context. During the wet season, tuft use on mounds and grazing lawn extent were greatest at the site with intermediate rainfall and foliar nutrients (Napi), where mammalian herbivore biomass was also highest. Differences in the ratio of tuft use between mound and matrix were also particularly pronounced here. Where herbivore biomass is high, it may lead to depletion of alternative high-quality forage patches in the savanna matrix, with termite mounds coming under greater pressure as animals are forced to utilise them. Tuft use on mounds decreased with decreasing herbivore biomass across sites, with the lowest levels of mound use recorded at the wettest site (Pretoriuskop).

Despite lower herbivore biomass and higher mound densities at the driest, most nutrient-rich site (Skukuza), tuft use in the savanna matrix was higher compared to Napi, with the lowest ratio of mound to matrix use here. In this relatively nutrient-rich savanna, nutrient availability

was higher in the savanna matrix and likely sufficient for herbivores during the wet season, with mounds being less important as foraging patches for maintaining populations. However, as nutritional content of grasses in the savanna matrix decreases (with increasing annual rainfall), nutritional differences between mound and matrix become more pronounced and the importance of mounds increases, with a higher ratio of mound to matrix use and a greater sphere of influence around mounds. Van der Plas et al. (2013) suggest that in high-nutrient savannas, browsers are not reliant on mound vegetation and can obtain sufficient nutrition in the savanna matrix. Our results provide some support for this notion in grazing herbivores, with less reliance on mounds in high-nutrient savanna. However, with grass on and around (1 m off) mounds at all three savanna sites containing higher levels of essential nutrients (N and P) than the savanna matrix, mounds were still always preferred as foraging sites. We hypothesise that mounds will be even less important as sources of high quality forage in very high nutrient sites (e.g. the basaltic plains of KNP or the nutrient-rich volcanic soils of east Africa, see also Cromsigt and te Beest 2014).

During the dry season, herbivores are under increased pressure to find resources with sufficient nutrients, with both tuft use and grazing lawn extent increasing on and around mounds at all sites. Differences in grazing pressure on mounds across sites were diminished, and grazers used termite mounds similarly at all sites. Grass nutritional value declines through the dry season (Treydte et al. 2008) and forage patches do not re-grow, placing pressure on grazers to locate resources (Owen-Smith and Novellie 1982). As a result, it is likely that during the dry season the matrix grasses at all sites no longer contain sufficient nutrients and many high-quality patches are exhausted, resulting in herbivores relying more heavily on mound vegetation (see also Grant and Scholes 2006).

Landscape scale influence of termite mounds

The sphere of influence, based on tuft use, around individual mounds demonstrates that termites affect herbivore foraging at scales greater than the extent of their mounds, and influence grazing patterns over as much as 30% of savanna landscapes. Levick et al. (2010b) measured termite influences on browsing herbivores up to 20 m into the savanna matrix at the end of the wet season (early May) at nutrient-poor Pretoriuskop. Our measurements for grazers in the same savanna site at a similar time of year were less, up to a maximum of 16 m from mounds. Woody plants have deeper, more extensive root systems than grasses with their roots extending well beyond their own canopy (Scholes and Archer 1997). It is likely that the larger rooting systems enable woody plants to access the nutrient and moisture enriched soil around termite mounds at greater distances than grasses, enlarging the sphere of influence that mounds have on browsing patterns. The direct sphere of mound influence on grass species assemblages is much lower (between 2 and 4 m) (Davies et al. 2014b) than the grazing patterns recorded here, indicating that cascading effects of termite mounds on savanna grass nutritional content are larger than the direct effects of mounds on grass species assemblages. The extent of grazing lawns around mounds, however, matched the extent of altered species assemblages more closely, suggesting a two-layered effect. Intense grazing around mounds (lawns) is spatially restricted to the distinct species assemblages around them, but enhanced, although less intense, grazing extends further into the savanna matrix.

Grazing lawns are recognised as important features in African savannas (Young et al. 1995, Archibald 2008, Hempson et al. 2014), and are initiated by disturbance (including termite activity) rather than large migratory herds in southern Africa (Cromsigt and Olff 2008). Termite activity, rather than grazing, has been shown to alter grass species assemblages around mounds (Okullo and Moe 2012a), but once altered communities are established, grazing herbivores maintain and enhance such differences (Okullo and Moe 2012b), contributing to grazing lawn formation (Cromsigt and Olff 2008). Accordingly, the larger grazing lawns throughout the year at Napi are likely a result of a combination of higher overall herbivore densities and lower mound densities, with associated higher grazing pressure generally and at mounds. Positive-feedback loops may then result, with termite activity leading to enhanced grazing that facilitates lawn establishment and causes herbivores to spend more time around mounds, adding nitrogen to the soil through increased levels of dung and urine, which further enhances the nutritional value of the soil and vegetation, and attracts herbivores. Similar positive-feedback loops between mammals and termites have been suggested previously and could be an important contributor to high herbivore densities (Freymann et al. 2010, Davies et al. 2012, Cromsigt and te Beest 2014). Indeed, the highest herbivore biomass in our study was recorded where mounds were most utilised by grazers (Napi), despite intermediate nutrient levels in the savanna matrix here.

Mounds became more important foraging patches for grazers during the dry season, with the sphere of influence (measured with tuft use) around them increasing at nutrient-rich Skukuza. In contrast, although mound use and grazing lawn extent increased at the wet, nutrient-poor site, Pretoriuskop, during the dry season, the sphere of influence and extent into the savanna matrix measured with tuft use decreased and was half the size compared to the wet season. Furthermore, grazing extent (tuft use into the matrix) was less here than at Skukuza, in contrast to wet season patterns. Mounds at Pretoriuskop are significantly smaller than at Skukuza (Davies et al. 2014a) and this may result in lower rates of soil erosion into the matrix, leading to smaller spheres of influence. Moreover, the much smaller mounds result in less nutrient-rich forage growing on them, which is likely to be depleted faster than the more abundant forage on the larger Skukuza mounds, forcing herbivores to seek forage elsewhere. Grazing lawn extent was greatest at all sites in the drier months, and largest at Pretoriuskop, indicating that mound grasses are still attractive to herbivores and consumed, providing further support for patch depletion, rather than nutrient depletion of mound grasses. At Skukuza, however, the larger mounds provide more forage, and herbivores are able to use them throughout the dry season. Patch depletion at mounds in nutrient-poor landscapes implies that herbivores here will be more dependent on other forage patches, or alternatively occur at lower densities or migrate. Indeed, such nutrient-rich patches have been described as

"limited intake resources" that provide highly nutritious food, but only in limited abundance (Owen-Smith 2002). Similarly, large savanna trees are important foraging patches for ungulates, but by themselves are not enough to sustain herbivore populations (Treydte et al. 2009).

Conclusion

Our findings demonstrate that termite mounds are preferred foraging sites across nutritionally different savanna types and thus enhance the value of savannas for grazing herbivores. By upscaling our results with LiDAR-estimated mound densities, we further demonstrate that the influence of *Macrotermes* mounds on savanna grazing patterns extends beyond the mound itself, influencing up to 30% of the landscape. Mounds thus act as keystone structures and contribute significantly to savanna heterogeneity. Cromsigt et al. (2009) suggest that habitat heterogeneity facilitates herbivore diversity and that high levels of heterogeneity may counterbalance effects of landscape fragmentation and declining reserve size. Areas with increased mound densities or larger termite mounds are thus likely to support larger and more diverse populations of mammalian herbivores and should be incorporated into measurements of habitat quality. However, the importance of termite mounds varies with landscape context (nutritional availability), mound size and density, and herbivore biomass, and is likely to be greatest in landscapes that are relatively nutrient-poor, and expressly where mounds are large enough (≥ ~1 m tall) to sustain high levels of herbivory throughout the year.

Acknowledgements – We thank Susan Trumbore, Iris Kuhlmann, Ines Hilke and Michael Rassler (Max Planck Institute for Biogeochemistry) for assistance and advice with the nutritional analyses, and David Knapp, Ty Kennedy-Bowdoin and Robin Martin for their contributions as members of the Carnegie Airborne Observatory. South African National Parks is thanked for logistical and scientific support and the DST-NRF Centre of Excellence for Invasion Biology and the South African National Parks/University of Pretoria Bursary for funding. Field work and application of the CAO data in South Africa is made possible by the Andrew Mellon Foundation, Grantham Foundation for the Protection of the Environment, and the endowment of the Carnegie Institution for Science. The Carnegie Airborne Observatory is supported by the Avatar Alliance Foundation, Gordon and Betty Moore Foundation, Grantham Foundation for the Protection of the Environment, W. M. Keck Foundation, the Margaret A. Cargill Foundation, Mary Anne Nyburg Baker and G. Leonard Baker Jr. and William R. Hearst III.

References

Anderson, T. M. et al. 2010. Landscape-scale analyses suggest both nutrient and antipredator advantages to Serengeti herbivore hotspots. – Ecology 91: 1519–1529.

Archibald, S. 2008. African grazing lawns – how fire, rainfall and grazer numbers interact to affect grass community states. – J. Wildlife Manage. 72: 492–501.

Archibald, S. and Bond, W. J. 2004. Grazer movements: spatial and temporal responses to burning in a tall-grass African savanna. – Int. J. Wildland Fire 13: 377–385.

Arshad, M. A. 1982. Influence of the termite *Macrotermes michaelseni* (Sjöst) on soil fertility and vegetation in a semi-arid savannah ecosystem. – Agro-Ecosyst. 8: 47–58.

Barton, K. 2010. MuMIn: multi-model inference. – R package ver. 0.13.17 <www.r-project.org>.

Bates, D. et al. 2007. The lme4 package. – R package ver. 2(1) <www.r-project.org>.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. – Springer.

Cromsigt, J. P. G. M. and Olff, H. 2008. Dynamics of grazing lawn formation: an experimental test of the role of scale-dependent processes. – Oikos 117: 1444–1452.

Cromsigt, J. P. G. M. and te Beest, M. 2014. Restoration of a megaherbivore: landscape-level impacts of white rhinoceros in Kruger National Park, South Africa. – J. Ecol. 102: 566–575.

Cromsigt, J. P. G. M. et al. 2009. Habitat heterogeneity as a driver of ungulate diversity and distribution patterns: interaction of body mass and digestive strategy. – Divers. Distrib. 15: 513–522.

Dangerfield, J. M. et al. 1998. The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. – J. Trop. Ecol. 14: 507–520.

Davies, A. B. et al. 2012. The pyrodiversity–biodiversity hypothesis: a test with savanna termite assemblages. – J. Appl. Ecol. 49: 422–430.

Davies, A. B. et al. 2014a. Spatial variability and abiotic determinants of termite mounds throughout a savanna catchment. – Ecography 37: 852–862.

Davies, A. B. et al. 2014b. Variable effects of termite mounds on African savanna grass communities across a rainfall gradient. – J. Veg. Sci. 25: 1405–1416.

Davies, A. B. et al. 2015. Data from: Termite mounds differ in their importance for herbivores across savanna types, seasons and spatial scales. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.b0b1c>.

Erpenbach, A. et al. 2013. The influence of termite-induced heterogeneity on savanna vegetation along a climatic gradient in west Africa. – J. Trop. Ecol. 29: 11–23.

Fox, J. et al. 2009. CAR: companion to applied regression, R package ver, 1.2-16 <www.r-project.org>.

Freymann, B. P. et al. 2010. Spatial and temporal hotspots of termite-driven decomposition in the Serengeti. – Ecography 33: 443–450.

Genz, A. et al. 2011. mvtnorm: multivariate normal and t distributions. – R package ver. 0.9-9991 <www.r-project.org>.

Gertenbach, W. P. D. 1983. Landscapes of the Kruger National Park. – Koedoe 26: 9–121.

Grant, C. C. and Scholes, M. C. 2006. The importance of nutrient hot-spots in the conservation and management of large wild mammalian herbivores in semi-arid savannas. – Biol Conserv 130: 426–437.

Hempson, G. P. et al. 2014. Ecology of grazing lawns in Africa. – Biol. Rev. 90: 979–994.

Hopcraft, J. G. C. et al. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. – Trends Ecol. Evol. 25: 119–128.

Hothorn, T. et al. 2008. Simultaneous inference in general parametric models simultaneous inference in general parametric models. – Biometrical J. 50: 346–363.

Jouquet, P. et al. 2004. Association between subterranean termites and grasses in a west African savanna: spatial pattern analysis shows a significant role for *Odontotermes n. pauperans*. – Appl. Soil Ecol. 27: 99–107.

Levick, S. R. et al. 2010a. Regional insight into savanna hydrogeomorphology from termite mounds. – Nat. Comm. 1: 65.

Levick, S. R. et al. 2010b. The spatial extent of termite influences on herbivore browsing in an African savanna. – Biol. Conserv. 143: 2462–2467.

Loveridge, J. P. and Moe, S. R. 2004. Termitaria as browsing hotspots for African megaherbivores in Miombo woodland. – J. Trop. Ecol. 20: 337–343.
Mobæk, R. et al. 2005. Termitaria are focal feeding sites for large ungulates in Lake Mburo National Park, Uganda. – J. Zool. Lond. 267: 97–102.
Moe, S. R. et al. 2009. Mound building termites contribute to savanna vegetation heterogeneity. – Plant Ecol. 202: 31–40.
Muvengwi, J. et al. 2013. Termite mounds may not be foraging hotspots for megaherbivores in a nutrient-rich matrix. – J. Trop. Ecol. 29: 551–558.
Okullo, P. and Moe, S. R. 2012a. Termite activity, not grazing, is the main determinant of spatial variation in savanna herbaceous vegetation. – J. Ecol. 100: 232–241.
Okullo, P. and Moe, S. R. 2012b. Large herbivores maintain termite-caused differences in herbaceous species diversity patterns. – Ecology 93: 2095–2103.
Owen-Smith, N. 2002. Adaptive herbivore ecology: from resources to populations in variable environments. – Cambridge Univ. Press.
Owen-Smith, N. and Novellie, P. 1982. What should a clever ungulate eat? – Am. Nat. 119: 151–178.
Parr, C. L. et al. 2004. Response of African savanna ants to long-term fire regimes. – J. Appl. Ecol. 41: 630–642.
Radford, I. J. and Andersen, A. N. 2012. Effects of fire on grass-layer savanna macroinvertebrates as key food resources for insectivorous vertebrates in northern Australia. – Austral Ecol. 37: 733–742.
Scholes, R. J. 1997. Savanna. – In: Cowling, R. M. et al. (eds), Vegetation of southern Africa. Cambridge Univ. Press.
Scholes, R. J. and Archer, S. R. 1997. Tree–grass interactions in savannas. – Annu. Rev. Ecol. Syst. 28: 517–544.
Smit, I. P. J. et al. 2007. Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. – Biol. Conserv. 136: 85–99.
Traoré, S. et al. 2008. Impact of *Macrotermes* termitaria as a source of heterogeneity on tree diversity and structure in a Sudanian savanna under controlled grazing and annual prescribed fire (Burkina Faso). – For. Ecol. Manage. 255: 2337–2346.
Treydte, A. C. et al. 2008. Improved quality of beneath-canopy grass in South African savannas: local and seasonal variation. – J. Veg. Sci. 19: 663–670.
Treydte, A. C. et al. 2009. Modelling ungulate dependence on higher quality forage under large trees in African savannahs. – Basic Appl. Ecol. 10: 161–169.
Treydte, A. C. et al. 2011. Grazing ungulates select for grasses growing beneath trees in African savannas. – Mamm. Biol. Z. Säugetierkunde 76: 345–350.
Van der Plas, F. et al. 2013. Functional traits of trees on and off termite mounds: understanding the origin of biotically-driven heterogeneity in savannas. – J. Veg. Sci. 24: 227–238.
van Wilgen, B. W. et al. 2000. A fire history of the savanna ecosystems in the Kruger National Park, South Africa, between 1941 and 1996. – S. Afr. J. Sci. 96: 167–178.
Whyte, I. J. et al. 2003. Kruger's elephant population: its size and consequences for ecosystem heterogeneity. – In: Du Toit, J. T. et al. (eds), The Kruger experience: ecology and management of savanna heterogeneity. Island Press, pp. 332–348.
Young, T. P. et al. 1995. Long-term glades in *Acacia* bushland and their edge effects in Laikipia, Kenya. – Ecol. Appl. 5: 97–108.
Zambatis, N. 2003. Determinants of grass production and composition in the Kruger National Park. – School of Appl. Environ. Sci., Univ. of Natal.

Supplementary material (available online as Appendix oik-02742 at <www.oikosjournal.org/appendix/oik-02742>). Appendix 1.